

Previous workers have often been strongly influenced by the geographic limitations of the taxa they were studying. But if geographic distribution is ignored and abundant material is examined, it is possible to recognize two morphologically distinct groups. To me, it seems most logical to recognize these as species, and to consider further variations as subspecific. Six subspecies of the two species are here accepted as distinguishable and are treated in this paper.

#### TAXONOMIC LITERATURE

The generic name *Joinvillea* first appeared in the "Atlas" to the *Botany of the Voyage of the Bonite* by Gaudichaud (1841<sup>1</sup>). The two binomials, *J. elegans* and *J. ascendens*, published by Gaudichaud have caused confusion, since the specimens and the locality information were lost and there were no written diagnoses. *Joinvillea elegans* was typified by detailed drawings of a fertile specimen and *J. ascendens* by drawings of a sterile specimen. However, in the absence of written descriptions the genus, and therefore also the species, were invalidly published as of 1841 and should be correctly dated 1861, the publication year of "Note sur la genre *Joinvillea* de Gaudichaud et sur la famille des Flagellariées" by Brongniart and Gris (Newell & Stone, 1967).

In the work of Brongniart and Gris, along with the generic description, are formal descriptions of Gaudichaud's two species, *Joinvillea elegans* and *J. ascendens*, and a new species *J. gaudichaudiana* from the Hawaiian Islands.

Hooker (1855) described a plant from the Île des Pins (New Caledonia) which he named *Flagellaria plicata*. He did not feel that it was sufficiently different from *Flagellaria* to place it in a separate genus, and apparently he was unaware of Gaudichaud's work, since he made no mention of it. This plant, which is a *Joinvillea* in the present concept of that genus, has since been considered a synonym of *J. elegans*, and the combination *J. plicata* was only recently made by Newell and Stone (1967). If the two taxa are the same, the epithet *plicata* should be applied, and *J. elegans* reduced to synonymy for reasons explained by Newell and Stone (1967).

Seemann (1868) made the combination *Flagellaria elegans* and considered *F. plicata* Hook. f. and *J. elegans* Gaud. as synonyms. Wawra (1875), however, disagreed and considered the establishment of the genus *Joinvillea* justified.

Hillebrand (1888) considered *Joinvillea adscendens* Gaud. (orthographic variant of *J. ascendens* Gaud.) as the name to be applied to the Hawaiian material and considered *J. gaudichaudiana* to be a synonym. He also pointed out that Wawra's description (Wawra, 1875) concurred with his belief that the Hawaiian material comprised only a single species. If these species are combined, as in the present treatment, Hillebrand's

<sup>1</sup> Publication date from Johnston (1944).

choice of *J. ascendens* must be followed according to Article 57, *International Code of Botanical Nomenclature* (Lanjouw, 1966).

Beccari (1902) described a new species, *Joinvillea borneensis*, from a specimen he collected at Gunong Wa, Sarawak, on the island of Borneo. Ridley (1905), apparently unaware of Beccari's paper, described a species, *J. malayana*, from West Malaysia, noting that it was found in Sarawak. Merrill (1921) and later workers have considered *J. malayana* a synonym of *J. borneensis*.

Engler (1930) recognized three species of *Joinvillea*: *J. elegans*, which he considered to occur in Fiji, Samoa, and New Caledonia; and *J. ascendens* and *J. gaudichaudiana*, both of which he credited to the Hawaiian Islands. He pointed out that the latter two species are not very different from each other.

Christophersen (1931) presented evidence for the reduction of *Joinvillea ascendens* to the synonymy of *J. gaudichaudiana*. However, the choice of Hillebrand, the first person to combine the species, must be followed. Christophersen also stated that *J. gaudichaudiana* differs from *J. elegans* mainly in shape and relative size of the tepals.

Christophersen (1935), described a new species, *Joinvillea bryanii*, from Savaii, Western Samoa. According to him, "It differs from *J. elegans* in the subequal perianth segments and from *J. gaudichaudiana* in the narrower, lanceolate segments." He indicated that *J. gaudichaudiana* also occurs in Western Samoa, both on Upolu and, with *J. bryanii*, on Savaii.

Backer (1951) recognized three species of *Joinvillea* but considered only the Malayan one, *J. borneensis*, in his paper. He considered *J. malayana* to be a synonym of *J. borneensis*.

It will be seen, then, that various authors have presented diverse interpretations of identities and limitations within the genus *Joinvillea*. My taxonomic conclusions will be indicated in the final portion of this treatment, after a consideration of morphological and other pertinent criteria.

#### MORPHOLOGICAL AND ANATOMICAL LITERATURE

Little anatomical or morphological work was published on *Joinvillea* prior to Smithson's paper in 1956. Arber (1925), in a morphological study of the monocotyledons, considered the leaf development of *J. elegans*. Solereder and Meyer (1929) briefly discussed the anatomy of the family.

Studies of pollen morphology such as those of Erdtman (1944, 1952) and Selling (1947), who indicated that pollen of *Joinvillea* is similar to that of grasses, inferred that, in this case, its study is more useful at the family or genus level than at that of the species.

Smithson (1956) carried out the most complete anatomical study of the Flagellariaceae, indicating several characters of possible taxonomic value. Among these is her report finding two different arrangements of

the vascular bundles in the leaf sheaths of *J. gaudichaudiana* and *J. borneensis*. In the latter species she found large and small bundles alternating in one layer near the surface, while in *J. gaudichaudiana* she reported four to five layers of bundles irregularly arranged and increasing in size toward the adaxial surface. She described the abaxial bundles of *J. gaudichaudiana* as embedded in a common sclerenchymatous sheath, while toward the adaxial surface each bundle had its own sheath. These appear to be marked differences which might be applied to the taxonomy of the entire genus.

The different types of trichomes found on the lamina of the two species by Smithson may provide another character of possible taxonomic value. She reported that *Joinvillea borneensis* has thick-walled trichomes especially prevalent opposite the rows of bulliform cells, and present on both surfaces; and that *J. gaudichaudiana* has similar thick-walled trichomes and also multicellular branching trichomes with thin-walled terminal cells.

Of the characters detailed by Smithson, these seem most striking for use as taxonomic criteria; but in reality they have only limited value, and one of them is based upon a misinterpretation, to be discussed later.

#### ACKNOWLEDGMENTS

The following abbreviations pertain to herbarium field series numbers used by some collectors: *BSIP* (British Solomon Island Plants); *SAN* (Forestry Department, Sandakan); *SAR* (Sarawak Forestry Service); and *SF* (Singapore Field Series).

In the course of this study herbarium material was examined from the institutions here cited with the indicated abbreviations: Arnold Arboretum of Harvard University (A); Bernice P. Bishop Museum (BISH); Herbarium Universitatis Florentinae (FI); Royal Botanic Gardens, Kew (K); Rijksherbarium, Leiden (L); New York Botanical Garden (NY); Muséum National d'Histoire Naturelle, Paris (P); and U.S. National Museum (US). I am indebted to the administrators of these herbaria for the loan of valuable specimens. I am equally indebted to the numerous institutions and persons in southeast Asia and the Pacific area without whose aid my field collections and study would have been impossible.

Acknowledgment is also extended to the Lyon Arboretum and the Department of Botany, University of Hawaii, for use of facilities; to Dr. George W. Gillett for suggesting the problem and for initial direction; to Dr. Charles H. Lamoureux and Dr. Yoneo Sagawa for serving as members of my thesis committee; to Dr. Albert C. Smith for serving as thesis committee chairman and for advisory comments; to the Center for Cultural and Technical Interchange between East and West (East-West Center) for field study expenses; and to my wife, Carol, for her patience and help with typing.

## FIELD STUDIES

Between August and November, 1966, observations and field collections were made throughout the range of the genus, and specifically at the following localities: West Malaysia at Gunong Hijau above Taiping, at Cameron Highlands, and at Fraser's Hill; Sabah, East Malaysia, between the town of Tamparuli and the Sabah National Park (SNP), and in the vicinity of the SNP; the British Solomon Islands Protectorate (BSIP), on northwestern Guadalcanal on the ridge above Hidden Valley; New Caledonia on the Plateau de Dogny and in the mountains southwest of the Plateau, on Mont Koghi, Route de l'Hermitage, along the road from the mouth of the Lembi Rivière to the Monts Kouanenoa, and on the Île des Pins; Fiji Islands on Viti Levu in Mba Province at Nandarivatu, in Serua Province along the road north of Ngaloa, and in Naitasiri Province along the Sawani-Serea Road; Western Samoa on Savaii southwest of Matavanu Crater and in the mountains above Samataitai, and on Upolu by Lake Lanutoo; and the Hawaiian Islands on the islands of Oahu, Molokai, Maui, and Hawaii.

To expedite reference to my own collections, they are designated by my field numbers preceded by the letter "N". These collections were supplemented by those of other collectors from the same areas and from several additional localities. The first set of my collections is deposited at the Bernice P. Bishop Museum, Honolulu, and duplicates have been distributed to other herbaria.

## VEGETATIVE CRITERIA

The shoots of *Joinvillea* vary in height and thickness. Height seems to be related to shading from surrounding vegetation; and plants of a given subspecies tend to be noticeably taller in shaded localities. The unbranched shoots of all taxa of *Joinvillea* grow erect from the root crown like clump-forming bamboo. Height and thickness of the shoots are of minor value in distinguishing the different taxa.

The glabrous stem and leaf sheath of *Joinvillea* typically have terete cross sections, but some New Caledonian specimens, of both *J. ascendens* subsp. *glabra*, and *J. plicata* subsp. *plicata*, were found with these parts appearing laterally compressed. Compressed shoots (leaf sheaths and stems) were found only in material from New Caledonia and appear to be correlated with shortened internodes (FIG. 2). This condition seems typical of subspecies *glabra*, although I found one plant of this subspecies with an intermediate shoot and one with an essentially terete shoot. It appears to be a genetically controlled trait rather than the result of ecological differences. Three collections of subspecies *glabra*, N199, N200, and N201, growing within 5 meters of each other, had terete, intermediate, and compressed shoot cross sections, respectively. Seedlings grown in Honolulu showed further evidence of this. These

seedlings, grown under identical greenhouse conditions from seed of a terete specimen of subspecies *plicata* (N190) and from a compressed specimen of subspecies *glabra* (N201), showed the characteristics of their respective parents. The N190 seedlings had terete shoots and long internodes, while the N201 seedlings had compressed shoots and shorter internodes (FIG. 2).

Since some specimens of subspecies *glabra* have terete shoots, the usual condition of compressed shoots cannot be used as an absolute criterion to separate it from the other subspecies of *Joinvillea ascendens*. In *J. plicata* subsp. *plicata* most specimens from New Caledonia have terete cross sections, but some laterally compressed specimens and some intermediates were also found. Therefore, the latter subspecies cannot be distinguished from *J. ascendens* subsp. *glabra* on this basis.

Smithson (1956) reported that the species *Joinvillea gaudichaudiana* (= *J. ascendens*) and *J. borneensis* differed in the vascular bundle arrangement of the leaf sheath. This difference was not substantiated by my study, in which leaf sheath cross sections were cut from two specimens of each of these subspecies. The sections were taken from four points along the leaf sheath and at each point all four specimens showed close similarity. The sections from the midpoints of both subspecies (FIG. 3A and B) were comparable to those which Smithson reported from the leaf sheath of subspecies *borneensis*, and none resembled those reported by her as representative of subspecies *ascendens*. However, sections were obtained similar to her cross sections of subspecies *ascendens*. These occurred, however, in the stems of both subspecies, not in the leaf sheaths (FIG. 3C and D).

Apparently the wide variation in leaf sheath anatomy indicated by Smithson was actually a difference between leaf sheath and stem. Numbers of vascular bundles and amounts of fibrous tissue varied somewhat in leaf sheaths and stems of the specimens which I studied, but the variation appeared closely related to the age and vigor of the material, and was not considered of diagnostic value.

Several specimens from each of the other subspecies were also sectioned. Each showed close similarity to the leaf sheath and stem sections of the previous material. Specimens with compressed shoots were also basically similar, except for a displacement of the vascular bundles corresponding to the shape of the shoot.

Another vegetative criterion investigated was the length of the leaf auricle. Christophersen (1931) pointed out the variability of auricle length in material he examined. This variability is due, in part, to the breakage of the auricle as it becomes dry and brittle in age. However, the maximum length attained in some subspecies is limited, and it is possible to exclude such taxa from consideration if long auricles are present.

The lamina of *Joinvillea* typically is linear-lanceolate, plicate, abaxially concave, acute to attenuate at the tip, constricted at the base, and scabrous along the margins. Although most of these characters are fairly uniform



FIG. 2. Seedlings showing terete and compressed shoots. Two pots at left, *J. plicata* subsp. *plicata* (N190), showing terete shoots and long internodes. Two pots at right, *J. ascendens* subsp. *glabra* (N201), showing compressed shoots and short internodes; the planes of compression of these two plants oriented at right angles to each other.

and of little diagnostic value, the types and frequencies of the trichomes occurring on the lamina are of some taxonomic significance.

Most trichomes on the lamina of *Joinvillea* leaves are found on the abaxial surface. Those found on the adaxial surface are of a particular type and will be discussed later. One part of the study concerns those trichomes distributed over the abaxial surface of the lamina, excluding the multicellular trichomes associated with major veins. These trichomes on the abaxial surface vary in type and frequency of occurrence. Unicellular trichomes and branched and unbranched multicellular trichomes occur in the genus. Sampling several leaves of each collection number showed that types and relative frequencies of trichomes are generally uniform on a given plant. On some plants trichomes are restricted to leaf areas bordering rows of bulliform cells. In FIGURE 4 such rows of cells (totaling about 0.15–0.25 mm. wide) pass vertically between the most widely spaced veins in each drawing. The midpoint of the lamina was chosen as the site for comparison and several samples were taken from each of my collections. Scoring was relative, and the terms rare, infrequent, frequent, and abundant were used to designate observed differences. Frequency and distribution of trichomes on the leaf surface was verified by examination of corresponding dried specimens. These detailed observations on my collections were supplemented by observations on loan material from various herbaria.

Trichome type and frequency vary greatly in some subspecies, but are fairly uniform in others. This character can be used to distinguish sterile Western Samoan material, since the only two subspecies found there differ greatly. The first of the two, *Joinvillea plicata* subsp. *bryanii*, is very uniform in the type and frequency of its trichomes, having abundant trichomes of the type indicated in FIGURE 4I. The other, *J. ascendens* subsp. *samoensis*, has rare trichomes as shown in FIGURE 4C. The greatest variation in trichomes is found in *J. plicata* subsp. *plicata*. In New Caledonia alone, trichomes of this subspecies range from rare to abundant and include the types illustrated in FIGURE 4E–I. This variation does not appear directly correlated with other characters or with type of habitat. *Joinvillea ascendens* subsp. *ascendens* from Hawaii, is also variable in trichome frequency, ranging from rare to abundant, but most material is in the frequent to abundant range. FIGURE 4D represents the usual type found in this subspecies.

A separate comparison was made of the branched and unbranched multicellular trichomes associated with the major abaxial laminar veins. Some data pertaining to these trichomes are given in descriptions to taxa, but should be used with caution as the ranges often vary greatly.

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FIG. 3, A–D. Leaf sheath and stem cross sections of *Joinvillea*. A, B, Leaf sheath cross sections at midpoint between auricle base and point of nodal attachment, showing vascular bundle arrangement and canals. A, *Joinvillea ascendens* subsp. *borneensis* (N153). B, *Joinvillea ascendens* subsp. *ascendens* (N137). C, D, Stem cross sections at midpoint between two nodes, showing vascular bundle arrangement and absence of canals. C, *Joinvillea ascendens* subsp. *borneensis* (N153). D, *Joinvillea ascendens* subsp. *ascendens* (N137).

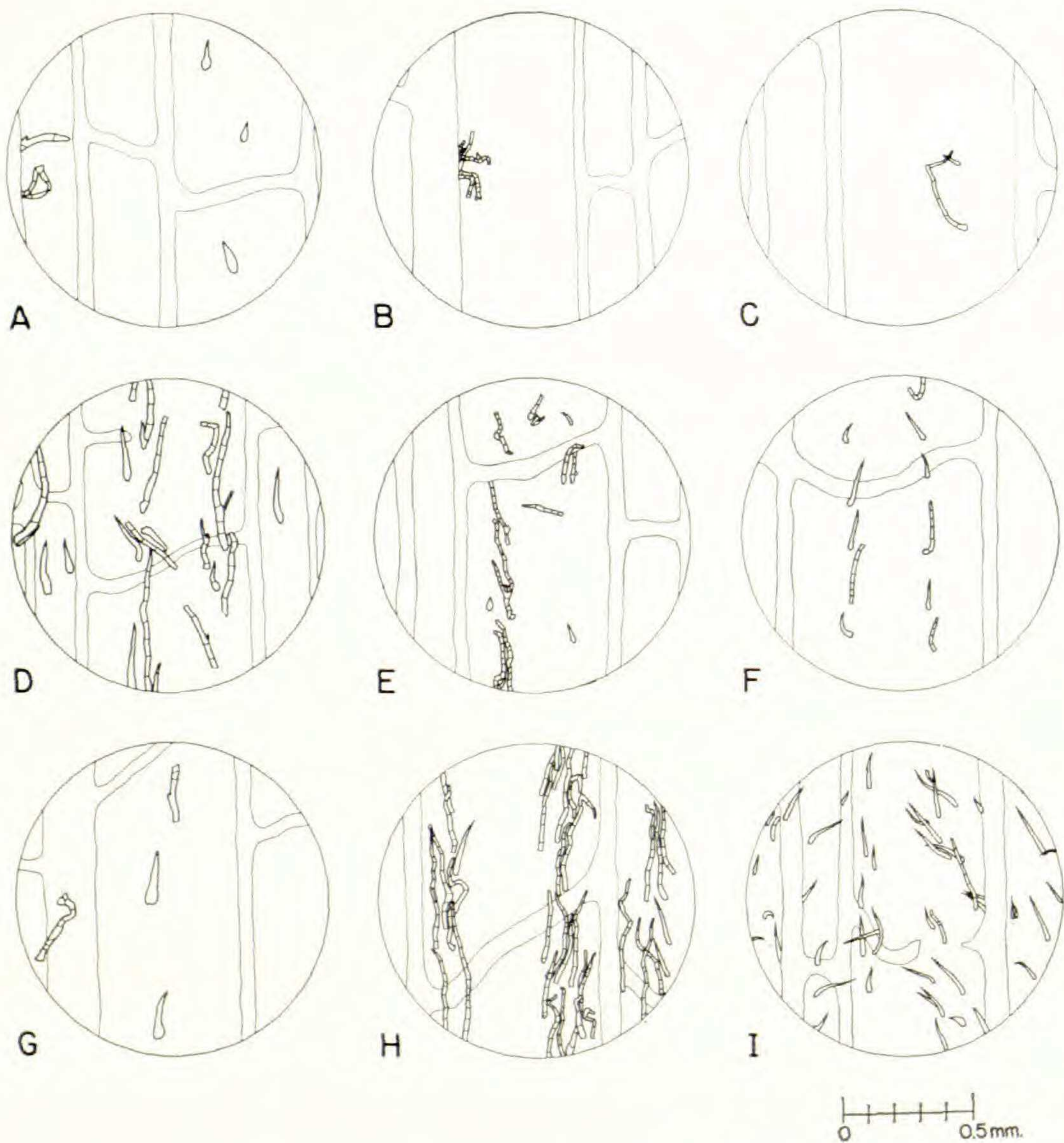


FIG. 4, A-I. Trichomes on the abaxial laminar surface of *Joinvillea*. A, Infrequent, mainly along veins and rows of bulliform cells. Trichomes predominantly unicellular. *J. ascendens* subsp. *borneensis*. B, Rare, mainly along veins. Trichomes predominantly multicellular and highly branched. *J. ascendens* subsp. *glabra*. C, Rare, mainly along rows of bulliform cells. Small unicellular and thin unbranched multicellular trichomes. *J. ascendens* subsp. *samoensis*. D, Abundant, distributed all over abaxial surface. Trichomes larger than in H and with a higher proportion of unicellular ones. *J. ascendens* subsp. *ascendens*. E, Frequent, mainly along rows of bulliform cells. Trichomes predominantly multicellular. *J. plicata* subsp. *plicata*. F, Frequent, mainly along rows of bulliform cells. Unicellular and multicellular trichomes equally apparent. *J. plicata* subsp. *plicata*. G, Infrequent, mainly along rows of bulliform cells. Unicellular trichomes larger than in A. *J. plicata* subsp. *plicata*. H, Abundant, distributed all over abaxial surface. Predominantly multicellular unbranched trichomes, but also a few unicellular ones. *J. plicata* subsp. *plicata*. I, Abundant, distributed all over abaxial surface. Trichomes predominantly thin and unicellular, but also a few thin multicellular ones. *J. plicata* subsp. *plicata* and *J. plicata* subsp. *bryanii*.



The last portion of the trichome study is a frequency evaluation of the thick stiff unicellular bristles that are mainly associated with the veins on both surfaces of the lamina. These bristles are oriented with their tips toward the leaf apex, and are easily detected by moving one's fingers over the surface from the apex toward the leaf base. For uniformity, scoring was based on the middle three-fourths of the lamina. Frequencies were scored by touch and expressed by the relative terms rare, infrequent, frequent, and abundant, which may be approximately quantified in the following manner: rare, 0-1 bristles/cm. on a few veins; infrequent, 1-2 bristles/cm. on some veins; frequent, 3-4 bristles/cm. on some veins; and abundant, 5-6 bristles/cm. on most veins. The frequency of the bristles in different subspecies was generally consistent but it was usually higher on seedlings.

This trichome study was undertaken partly because Smithson (1956) indicated that the types occurring on Hawaiian collections differed from those on the Malayan collections. She reported finding "thick-walled spines" (better referred to as bristles) on the lamina of a Malayan specimen, and these plus spiny multicellular branching hairs on a Hawaiian plant. However, after examining several specimens from each area, I have concluded that both types occur on material from both areas and on plants collected throughout the range of the genus. There is notable variation in type, frequency, and distribution of the trichomes over the lamina, but presence or absence of multicellular trichomes cannot be considered a valid criterion for distinguishing the two taxa mentioned above.

Although the leaf trichomes are variable, they are useful in delimitation of some taxa. This use is mainly at the subspecific level. However, in New Caledonia or Western Samoa, where both species occur side by side, it is possible to determine sterile specimens on the basis of trichome type, frequency, and distribution.

#### REPRODUCTIVE CRITERIA

The inflorescence of *Joinvillea* is a large, usually erect, three to five times branched, terminal panicle measuring 10-40 cm. long from the lowest branch to the apex, and 8-40 cm. wide. Inflorescence branch diameter is particularly useful in separating subspecies *ascendens* from all other subspecies. Its branches are usually larger in diameter and in this respect overlap only slightly with the other subspecies. Diameter measurements were made in two places: on a primary branch of the inflorescence midway between the rachis and the branch tip, and about 0.5 cm. from the tip of the ultimate branchlets. Data are presented in the key and descriptions.

The flowers which are sessile in the axils of fragile lanceolate bracts have six equal stamens and three fused carpels and do not seem to vary in the two species.

The size and especially the shape of the tepals are diagnostic, the shape of the outer tepals being the primary character of value for species

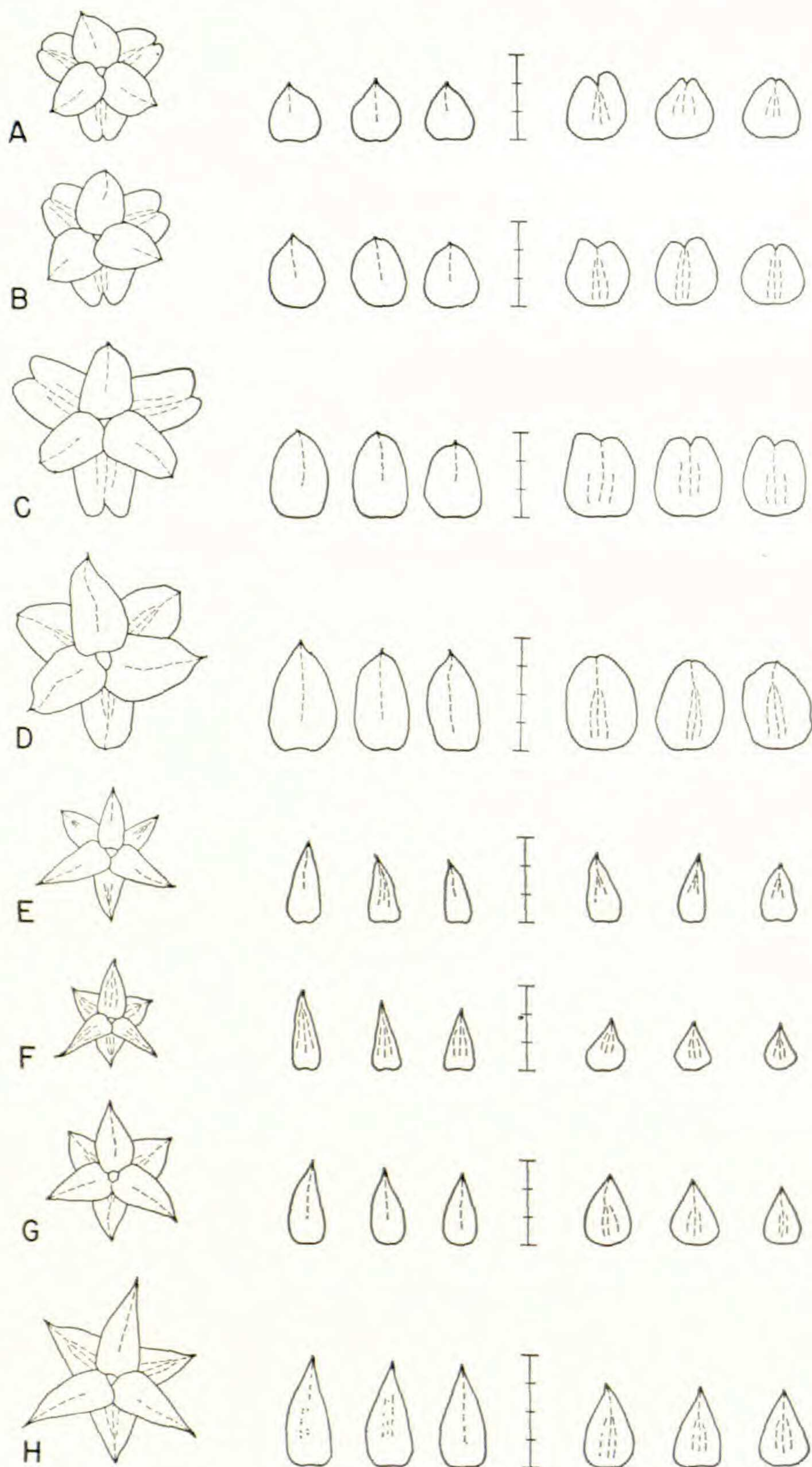


FIG. 5, A-H. Tepal shapes of *Joinvillea*. Drawings on left show abaxial view of flattened perianth. Left of scale, outer tepals; right of scale, inner tepals. Dashed lines are visible veins. *Joinvillea ascendens*, A-D. A, Subsp. *borneensis* (N143), from Sabah, East Malaysia; B, Subsp. *glabra* (N193), from Plateau de Dogny, New Caledonia; C, Subsp. *samoensis* (N239), from Upolu,

determination. Camera lucida drawings in FIGURE 5 illustrate representative tepals of the species and subspecies recognized in this treatment. The basic difference in shape is obvious, *Joinvillea ascendens* having ovate to orbicular-ovate outer tepals and orbicular-ovate inner tepals, while *J. plicata* has deltoid-lanceolate outer tepals and deltoid-lanceolate to ovate inner tepals. The membranaceous tepal edges of both species commonly shatter in age. Tepals of both species are adaxially concave (and abaxially convex), especially in the flowering stage, becoming spread and somewhat flattened as the fruit develops distally.

The bases of the tepals are thickened in both species, but the amount of thickening is difficult to assess in dried material. This basal tissue is thicker in the outer than in the inner tepals of a given specimen. The veins are usually obscured in the basal portions of the tepals, and therefore only the visible portions of the veins are represented by the dashed lines in FIGURE 5. Clearing and staining is usually necessary to show the continuation of the veins into the base of each tepal.

Venation in the outer tepals of *Joinvillea ascendens* (FIG. 5A-D) typically consists of one central vein, although sometimes one or two weakly expressed additional traces were present. The central vein extends from the tepal base to the apex and into the tip; however, the tip is often lost as the tepals become brittle and shatter in age. Before shattering occurs, the outer tepal tips of subspecies *borneensis* and *glabra* are usually mucronulate or sometimes mucronate. Reflexed mucronate tips were also observed on some tepals of these subspecies, but they are not as pronounced as in subspecies *ascendens*, where a strongly reflexed mucronate tip is normally present. Subspecies *samoensis* also bears a reflexed mucronate tip, but it is not usually as prominent as in subspecies *ascendens*. The outer tepals of *J. ascendens* occasionally split in age.

In *Joinvillea plicata* subsp. *plicata* the outer tepals often have one or two lateral veins, and in some specimens these laterals are as prominent as the midvein. Gradation from one to three prominent veins is often found in a given population and sometimes on a single plant. Therefore, it does not seem appropriate to recognize another subspecies on the basis of this variation. Subspecies *bryanii* normally has only a single midvein in the outer tepals, although one or two weakly expressed lateral veins are occasionally present. The outer tepals of both subspecies of *J. plicata* have acute to acuminate, not mucronate, tips, although the central vein does extend to the apex.

The inner tepals of *Joinvillea ascendens* normally have three veins, a central one and two weaker laterals. The latter sometimes unite with the central vein near the apex (FIG. 5A-D). The central vein of the

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Western Samoa; D, Subsp. *ascendens* (N261), from Molokai, Hawaii. *Joinvillea plicata*, E-H. E, Subsp. *plicata* (N176), from Guadalcanal, BSIP; F, Subsp. *plicata* (N189), from Mont Koghi, New Caledonia; G, Subsp. *plicata* (N227) from Serua Province, Viti Levu, Fiji; H, Subsp. *bryanii* (N251), from Savaii, Western Samoa.

Each scale division = 1 mm.

inner tepals extends to the apex but does not form a noticeable projection, since the tepals usually split, forming a retuse or emarginate tip. Splitting of the inner tepals which is most prevalent in subspecies *ascendens* may be related to the flattening of the tepals by the fruit, since when mature the fruit of this subspecies is dorsiventrally flattened and larger than that of the others. The inner tepals of *J. plicata* have three veins which unite below the acute apex of the tepal. In both subspecies the midvein extends to the normally entire apex but does not form a mucro.

Tepal shape was also evaluated by expressing shape as a ratio of length to width. Results obtained are presented as ranges of ratios in the descriptions and key. The ratios indicate greater variation in *Joinvillea plicata* and reinforce the species delimitations, since little overlap occurs between species. Within *J. plicata* there is a tendency for subspecies *bryanii* to have higher inner tepal ratios than subspecies *plicata*; however, there is considerable overlap. Within *J. ascendens* there is a tendency for subspecies *ascendens* to have higher ratios for both inner and outer tepals than does subspecies *samoensis*. Christophersen (1935) considered the Hawaiian material (subspecies *ascendens*) and the Western Samoan material (subspecies *samoensis*) to be the same. However, the tendency for higher ratios in the Hawaiian material, when considered with other characters, suggests that material from these two areas should be recognized as distinct subspecies.

Within their respective species, subspecies *ascendens* and subspecies *bryanii* have the longest tepals, and therefore the upper limits of their ranges of length can be used with some confidence for determination.

Fruit morphology indicates tendencies of difference between some of the taxa. Fruit diameter ranges were obtained using a dissecting microscope equipped with an ocular micrometer. Only fruits containing two or three seeds were measured. Fruits normally have three seeds, but when two of these are aborted the fruits are greatly reduced in size. Fruits measured were either fresh, preserved in FAA (formalin-acetic acid-alcohol), or boiled in water until they approximated the fresh condition. Much overlap occurs among taxa, but the extremes in diameter are sometimes useful.

Fruit shape was expressed as a ratio of diameter to height, exclusive of the perianth and style. The ratios indicate the degree of dorsiventral flattening, high values indicating a flattened fruit and low values a more globose fruit. These values also overlap greatly, but are sometimes useful.

As the fruit matures the feathery stigmas normally break off and are lost, leaving short styles. This occurs in all taxa except *Joinvillea ascendens* subsp. *ascendens*, where the styles appear to be absent in the fruiting stage or at least do not protrude above the fruit. This character is helpful in distinguishing this subspecies from subspecies *samoensis*, which usually has noticeably protruding styles.

Tepal shape is most useful as a diagnostic character at the specific level. The other criteria are more useful at the subspecific level.

## CYTOLOGICAL CRITERIA

Chromosome counts were obtained from material collected in each of the geographic areas I visited. Results were obtained mainly from microsporocytes. These were fixed in the field in a 3:1 mixture of absolute ethanol and glacial acetic acid, and later prepared by the aceto-orcein squash technique. One somatic count was obtained from root tips of seedlings grown in Honolulu, from New Caledonian seed. In each case the count was verified in several cells, and in all material counted, the haploid number was 18 and the diploid number 36. Counts were obtained from the collections indicated in TABLE 1. Among the meiotic configurations studied, no significant differences were observed; FIGURE 6 illustrates a representative chromosome complement. A count has not yet been obtained for *J. ascendens* subsp. *samoensis*.

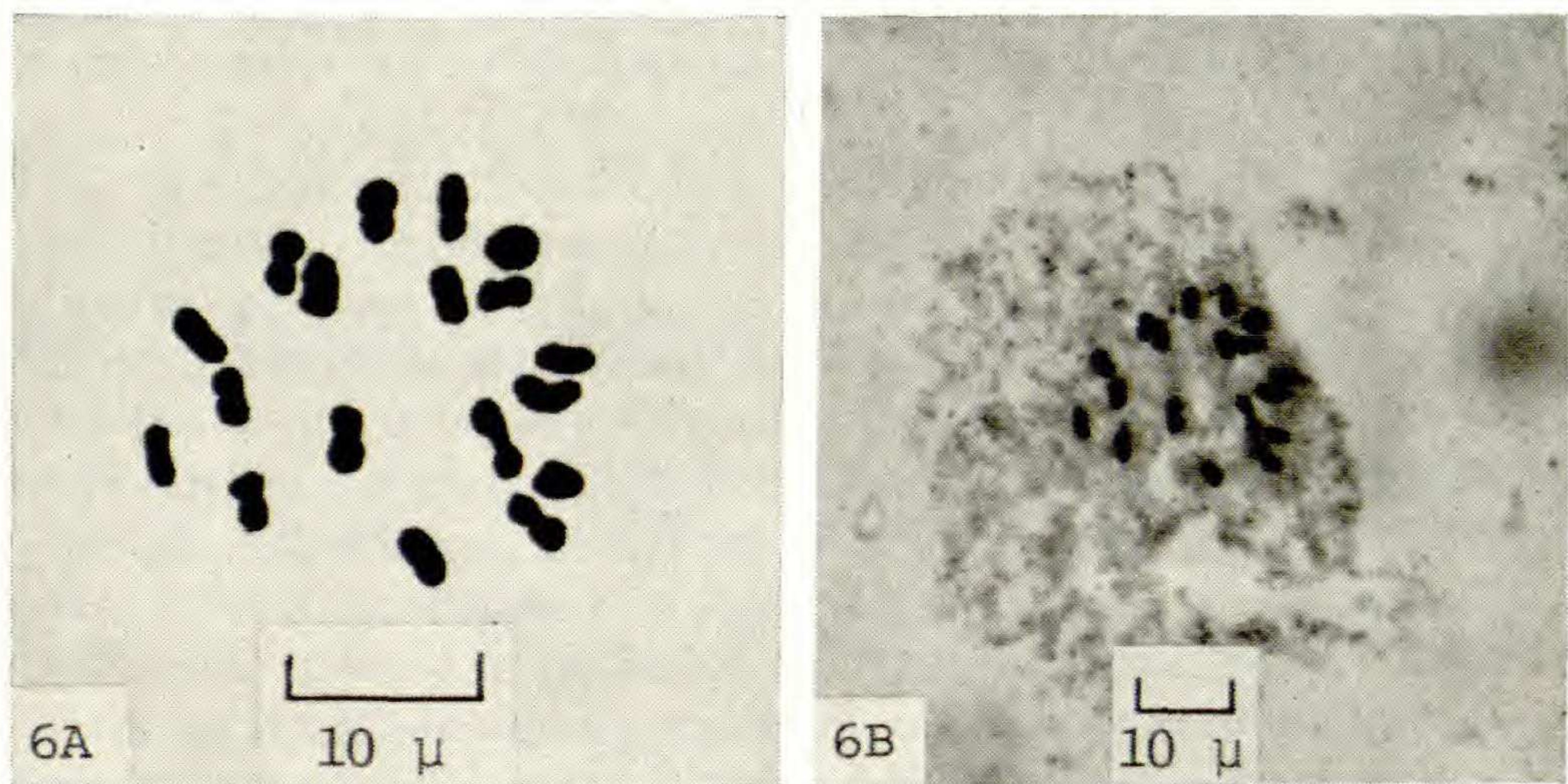


FIG. 6, A and B. Haploid chromosome complement of *Joinvillea*. A, Camera lucida drawing of the haploid chromosome complement ( $n = 18$ ) from a microsporocyte of *J. plicata* subsp. *plicata* (N232); specimen collected north of Ngaloa, Serua Province, Viti Levu, Fiji. B, Photograph of the actual cell drawn in FIG. 6A.

In the related genus *Flagellaria*, Shetty and Subramanyam (1964) reported a haploid number of 19 and a diploid number of 38 in *F. indica* L. The presence of the additional chromosome pair in *Flagellaria* supports its consideration as a genus distinct from *Joinvillea*. Separation of taxa on the basis of chromosome number cannot be made within the latter genus. The constancy of chromosome number within *Joinvillea* may be considered evidence of close relationships within the genus.

In summarizing this discussion of the various criteria studied, the approximate order of their usefulness in delimiting the taxa may be mentioned: shape of outer tepals, type and frequency of trichomes, size of tepals, diameter of inflorescence branches, size of style on mature fruit, size of fruit, and size of inflorescence. The combined use of these characters and others of lesser value permits recognition of taxa that seem to possess stability.

## DISCUSSION AND CONCLUSIONS

Several field observations were made on the possible means of pollination and dispersal for *Joinvillea*. Bees or wind, or both, may play a role as pollinators. Bees were the only insects observed on the flowers of *Joinvillea*. The observation was made on plants of *J. plicata* subsp. *plicata* in the Monts Kouanenoa area, New Caledonia. Ants were seen on the leaves of plants from various areas, but not on the flowers. Ants were commonly observed on flowers and stems of the related genus *Flagellaria* and may play a role in its pollination.

Self or cross pollination in *Joinvillea* might also be accomplished by wind. The filaments extend the mature anthers above the tepals to about the same height as the feathery stigmas, and since the stigmas and filaments are somewhat lax, the anthers and the stigmatic surfaces may easily contact each other as they move in the wind. The extruded anthers and stigmas also would provide ample opportunity for cross pollination by wind.

Dispersal is probably accomplished by birds, as suggested by Ridley (1930). The inflorescence is high on the plant and the fleshy, brightly colored fruits are readily visible to passing birds. However, I have never observed birds on the plants, nor do I know of any record of such an observation. The only tenable alternative to dispersal by birds is dispersal by high velocity storm winds. The fruits have no particular adaptation to wind dispersal, but they are light enough so that this may be a possibility.

Dispersal by man or sea is not probable for *Joinvillea*. Man can be logically excluded because no native uses for *Joinvillea* have been recorded. The stem of the related genus *Flagellaria* is sometimes used in Samoa for house construction as a stick to which thatch is tied (Christophersen, 1935), and in southeast Asia for basketwork, and for making hair-wash and medicinal applications (Backer, 1951). The application of the same native name to both genera has caused some confusion. Sea dispersal can be ruled out for two reasons. First, both fresh and dry seeds sink immediately, or shortly after placement in salt water, and second, the genus is found almost exclusively as a highland or inland plant, except in New Caledonia, where it sometimes occurs at quite low elevations, but not on the beach.

The seeds of all subspecies germinate readily even after being kept for as long as six weeks in an air dry condition. This would allow ample time for dispersal despite the large distances involved. From my experience in germinating seed and growing these plants, the main problem appears to be survival of the seedling stage.

There is some evidence for suggesting that interspecific crossing may be occurring in New Caledonia. Plants with compressed shoots are known to occur only on that island. My observations of adjacent plants, one with terete and one with compressed shoots, and observations of seeds from each developing into the parental type (FIG. 2), suggest that the

trait is genetically controlled. Since compressed and terete shoots occur in both species, the trait either originated by mutation in one species and was introduced to the other by interbreeding, or originated separately in both species. The probability of the former occurring certainly exceeds that of the latter. If interspecific crossing is occurring in these plants, it has not noticeably affected tepal shape, the two basic shapes being clearly separable in all material so far examined. The conspicuous success of *Joinvillea* in New Caledonia may be due to heterosis, but as yet there is no conclusive evidence of this. Experimental hybridization would be necessary to test this hypothesis.

#### SYSTEMATIC TREATMENT

*Joinvillea* Gaud. ex Brongn. & Gris, Bull. Soc. Bot. France 8: 268. 1861.

*Flagellaria* subgenus *Chortodes* Hook. f., Hook. Jour. Bot. Kew Gard. Misc. 7: 200. tab. VI. 1855. Type species *Flagellaria plicata* Hook. f.

Erect rhizomatous perennial herbs with few to numerous shoots, 1.5–5.5 m. high. Stem simple, terete or bilaterally compressed, hollow except at nodes, smooth, hard, glabrous, 4–14 mm. in greatest diameter at distal nodes, the distal internodes 2–14 cm. long (the distance between consecutive auricles), increasing in length toward base. Leaf sheath covering internode, open, terete or bilaterally compressed, smooth, firm, with vestiture on upper part, glabrous in age, faintly and closely nerved and striated, nerves converging at base of lamina, margins scarious; ligule diminutive; auricles 2, thinner than sheath, appressed against shoot, oblong with rounded to acute apex to subulate, smooth, faintly and closely nerved and striated, scarious at margin, 2–90+ mm. long, often withering and breaking in age, then sometimes 1 mm. or less in length. Lamina linear-lanceolate, constricted at base, abaxially concave, somewhat stiff, usually with abaxial vestiture and with bristles on both surfaces, margins scabrous, veins prominent on both surfaces, apex acute to attenuate but often withering in age, 7–15 longitudinal plications on each side of midrib, 48–100 cm. long and 4.5–20 cm. broad when flattened. Inflorescence a terminal panicle, erect, sometimes drooping in fruit, pyramidal, 3–5 times branched, 10–40 cm. long from proximal branch to apex and 8–40 cm. broad; rachis and branches with vestiture, branches (especially thinner ones) sinuous, primary branches (in dried condition) 0.7–2 mm. in diameter at midpoint, ultimate branchlets 0.3–0.9 mm. in diameter 5 mm. from tips; peduncle bract triangular to linear, membranous, early withering and caducous, sometimes to ca. 25 cm. long; bracts subtending branches triangular, membranous, early withering and caducous, mostly 0.5–3 cm. long; bracteoles subtending flowers triangular to subulate, membranous, early withering and caducous, mostly 1–4 mm. long. Flowers bisporangiate, actinomorphic, sessile on thickenings of the branchlets. Tepals 6, alternate in 2 series, hypogynous, persistent, free or slightly adnate at base, imbricate, spreading in fruit, adaxially concave, scarious or

chartaceous, base (especially of outer tepals) thickened, apex sometimes splitting in age, margins sometimes minutely ciliate; outer tepal (flattened) ovate to orbicular-ovate with a mucronulate to mucronate sometimes reflexed tip, or deltoid-lanceolate with an acute to acuminate apex, with 1 central vein and sometimes 1 or 2 laterals, 1.1–3.1 times longer than broad, 1.7–4.1 mm. long and 0.8–2.2 mm. broad; inner tepal orbicular-ovate with  $\pm$  truncate apex, often becoming retuse or emarginate in age, or deltoid lanceolate to ovate with an acute to acuminate apex, with 1 central vein and usually 2 laterals which sometimes unite with the central one below the apex, 0.8–2 times longer than broad, 1.5–3.5 mm. long and 0.8–2.6 mm. broad. Stamens 6, free, hypogynous or slightly adnate to tepal bases; filament filiform, ca. 2–4 mm. long at anthesis; anther oblong, sagittate at base, retuse at apex, basifixed with a narrow connective, bilocular and exerted at anthesis, opening laterally by 2 longitudinal slits, ca. 2 mm. long. Ovary superior, conoidal, with 3 fused carpels; locules 3; ovule solitary in each locule, orthotropous, pendulous from central axis, not basally attached; styles 3, free or slightly connate at base, linear, tapering distally, becoming obscured by developing stigmas; stigmas 3, linear when immature, becoming exerted, feathery, and papillate, somewhat persistent on fruit. Fruit indehiscent, drupaceous, glabrous, globose to somewhat dorsiventrally flattened when fresh, triquetrous (especially when dry), at first green, becoming red, red-orange, or brown-black at maturity, 1–1.7 times broader than high (to base of style and exclusive of perianth), 3.3–6 mm. in diameter (2- or 3-seeded and fresh); exocarp thin, sometimes becoming crustaceous; mesocarp fleshy; endocarp hard and bony. Seeds 3 or fewer by abortion, globose, rugulose, 1.5–2 mm. in diameter; endosperm copious; embryo minute, lenticular.

**TYPE SPECIES:** In Newell and Stone (1967) the type species of the genus *Joinvillea* was indicated as *Flagellaria plicata* Hook. f. Upon reconsideration, however, this seems incorrect. Although the epithet *plicata* dates from 1855 and is, therefore, the oldest validly published epithet now referable to *Joinvillea*, it was not considered by Brongniart and Gris (1861) in the first valid publication of the generic name. The type species of *Joinvillea* must be chosen from among the three species validly published by Brongniart and Gris in their 1861 treatment. Since Brongniart and Gris ascribed the genus to Gaudichaud (1841), it seems logical to select one of Gaudichaud's species as the type. The more fully illustrated *J. elegans* is herewith indicated as the appropriate lectotype for the genus *Joinvillea*. As pointed out in Newell and Stone, the plates published by Gaudichaud cannot serve as a valid generic description because no description is supplied or referred to, and a plate with analytic illustrations serves only to validate a new monotypic genus. Since the genus was invalidly published by Gaudichaud (1841), the two species, *J. ascendens* and *J. elegans*, illustrated in his plates are also invalidly published as of 1841.

**DISTRIBUTION.** The genus *Joinvillea* is distributed from West Malaysia



to Western Samoa and north to the Hawaiian Islands (FIG. 1); apparently a discontinuous distribution since there are no records from eastern Indonesia, New Guinea, or northern Australia. It occurs at elevations from near sea level to 1,920 meters, usually at the forest edge or in other partially open localities with ample light but some protection by other vegetation. The plants seem to be associated with moist, well-drained soils, and are often found on banks above streams or on slopes in areas of heavy rainfall.

When a wide selection of *Joinvillea* specimens is examined, basic tepal shape, particularly the shape of the outer tepals, appears to be the only clearly discontinuous character. Because this character seems stable, I think it forms an adequate basis for distinction of species. It can be used confidently without locality or other field data. Frequency of bristles on the adaxial laminar surface generally is correlated with tepal shape but is less precise as it must be expressed in relative terms. Further variation in these and in other characters is more appropriately applied at the subspecific level.

#### KEY TO THE SPECIES AND SUBSPECIES

1. Tepals usually splitting in age; outer tepals ovate to orbicular-ovate with a mucronulate to mucronate sometimes reflexed tip, 1.1–2 times longer than broad; bristles on the adaxial laminar surface usually rare to frequent. . . . . 1. *J. ascendens*.
2. Fruit 4.1–5.8 mm. in diameter; inflorescence mostly villous; outer tepals usually mucronate, often reflexed; inner tepals 1.9–3.5 mm. long.
  3. Stem 5–9 mm. in diameter at distal nodes; auricles to ca. 31 mm. long; ultimate inflorescence branchlets 0.4–0.9 mm. in diameter, 5 mm. from tips; outer tepals 2.7–4 mm. long; inner tepals 2.6–3.5 mm. long; styles not evident on fruit; Hawaiian Islands. . . . . 1a. subsp. *ascendens*.
  3. Stem 4–6 mm. in diameter at distal nodes; auricles to 6 mm. long; ultimate inflorescence branchlets 0.3–0.5 mm. in diameter, 5 mm. from tips; outer tepals 2.1–3 mm. long; inner tepals 1.9–3 mm. long; styles persistent on fruit; Samoa. . . . . 1b. subsp. *samoensis*.
2. Fruit 3.3–4.8 mm. in diameter; inflorescence mostly with erecto-patent short stiff trichomes; outer tepals usually mucronulate, rarely reflexed; inner tepals 1.8–2.6 mm. long.
  4. Stem and sheath terete, the distal internodes 5–11.5 cm. long; auricles mostly oblong with rounded apex; lamina 5–14 cm. broad, with 9–13 plications on each side of midrib, the bristles infrequent to frequent on both surfaces; southeast Asia and Ponape. . . . . 1c. subsp. *borneensis*.
  4. Stem and sheath bilaterally compressed, rarely terete, the distal internodes 3–6 cm. long; auricles mostly subulate; lamina 4.5–7 cm. broad, with 7–9 plications on each side of midrib, the bristles rare on both surfaces; New Caledonia. . . . . 1d. subsp. *glabra*.
1. Tepals usually not splitting in age; outer tepals deltoid-lanceolate with an acute to acuminate tip, 1.7–3.1 times longer than broad; bristles on the adaxial laminar surface usually frequent to abundant. . . . . 2. *J. plicata*.

5. Stem and sheath terete to bilaterally compressed; auricles oblong, rounded at apex, sometimes subulate, mostly straight; lamina with acute to attenuate apex; outer tepals 1.7–3.6 mm. long; inner tepals 1.1–3.1 mm. long; Solomon Islands, New Caledonia, New Hebrides, and Fiji. . . . . 2a. subsp. *plicata*.
5. Stem and sheath terete; auricles somewhat oblong, rounded to acute at apex, the apex mostly curving away from ligule; lamina with attenuate apex; outer tepals 2.9–4.1 mm. long; inner tepals 2.5–3.3 mm. long; Samoa. . . . . 2b. subsp. *bryanii*.

1. *Joinvillea ascendens* Brongn. & Gris, Bull. Soc. Bot. France 8: 269. 1861.

Erect herb, 1.5–5 m. high; auricles to ca. 40 mm. long; lamina with variable trichome types on abaxial surface, bristles on adaxial surface rare to sometimes frequent, 7–13 plications on each side of midrib, 48–79 cm. long and 4.5–16 cm. broad when flattened. Tepal apex usually splitting in age; outer tepals ovate to orbicular-ovate with a mucronulate to mucronate sometimes reflexed tip, with 1 central vein and very rarely 1 or 2 weakly expressed lateral veins, 1.1–2 times longer than broad, 1.7–4 mm. long and 1.4–2.2 mm. broad; inner tepals orbicular-ovate with the apex somewhat truncate and often becoming retuse or emarginate in age, 0.8–1.7 times longer than broad, 1.8–3.5 mm. long and 1.6–2.6 mm. broad. Styles sometimes not evident on fruit; fruit 3.3–5.8 mm. in diam.

The species *Joinvillea ascendens* is here recognized as being composed of four subspecies. Because tendencies of morphological differences among these subspecies are correlated with geography, it seems logical to consider them at this rank rather than at varietal level. The latter rank is better ascribed to variation within a single geographic area.

1a. *Joinvillea ascendens* subsp. *ascendens* FIG. 4D; FIG. 5D.

*Joinvillea ascendens* Gaud. Atlas, Voy. Bonite, pl. 39 & 40, fig. 1–6. 1841, *nomen nudum*; Brongn. & Gris, Bull. Soc. Bot. France 8: 269. 1861; Wawra, Flora 58: 248. 1875; Hillebrand (as *J. adscendens*), Fl. Hawaiian Isl. 447. 1888.

*Joinvillea gaudichaudiana* Brongn. & Gris, Bull. Soc. Bot. France 8: 269. 1861; Christophersen, Bishop Mus. Occ. Pap. 9(12): 5. 1931, Bishop Mus. Bull. 128: 46, p.p. 1935.

Erect herb, 3.5–5 m. high; stem terete, 5–9 mm. in greatest diam. at distal nodes, the distal internodes 5–13 cm. long; sheath terete; auricles to ca. 31 mm. long (mostly 20 mm. or less), oblong, rounded to slightly acute at apex; lamina with 9–13 plications on each side of midrib, 8–16 cm. broad; unicellular and multicellular trichomes on abaxial laminal surface rare to abundant (mostly frequent); bristles rare to infrequent on both surfaces. Inflorescence villous with a few erecto-patent short stiff trichomes, primary branches 1–2 mm. in diam. at midpoint, ultimate

branchlets 0.4–0.9 mm. in diam. 5 mm. from tips; outer tepals 2.7–4 mm. long, with a mucronate usually reflexed tip; inner tepals 2.6–3.5 mm. long. Styles not evident on fruit; fruit 4.6–5.8 mm. in diam.

TYPE: Kauai or Niihau, Hawaiian Islands, *Remy 156 A* (P lectotype) 1851–1855. Gaudichaud's figures (Gaudichaud, 1841) of *Joinvillea ascendens* are of incomplete material and accordingly could not have been the only basis for the description of this taxon by Brongniart and Gris (1861). Therefore it seems best to choose as lectotype the specimen cited by Brongniart and Gris, *Remy 156 A*. The specimen selected is in mature fruit. Although its label bears the locality "Kauai au Nihau" (Niihau), Kauai is probably correct as I know of no other record of *Joinvillea* from Niihau.

LOCAL NAME. Called "ohe" in Hawaiian, a name also applied to several other native plants and to bamboo.

DISTRIBUTION. Endemic to the Hawaiian Islands, occurring on Kauai, Oahu, Molokai, Maui, and Hawaii from 300 to 1,250 meters elevation. Plants rare, usually occurring as widely separated individuals on ridges, in forests, and along intermittent streams. Seedlings rarely observed.

Hawaiian Islands. KAUAI: Kokee, Halemanu, *Degener 30212* (BISH); Waipao Valley and Ridge, *Forbes & Dole 42 K* (BISH); Kilauea, Ka Loko Reservoir, *Forbes 564 K* (BISH); Hii Mts., *Forbes 623 K* (BISH); Lehue, *Mann & Brigham 330* (A, BISH, NY, US). KAUAI OR NIIHAU: *Remy 156 A* (P lectotype). OAHU. Waianae Mts.: Mt. Kaala, *Macrae s.n.* (A); Puu Hapapa, *St. John 10414* (BISH); below ridge e. of Puu Hapapa, *Christophersen 1286* (BISH); valley e. of Puu Hapapa, *N137* (*Newell 137*); Schofield side of Puu Kanehoa, *Beardsley s.n.* (BISH). Koolau Mts.: Laie, *Guppy s.n.* (K); Kawailoa Trail, middle forest, *N257*; Paalaa-Kawailoa divide, Puu Peahinaia, near crest of wooded ridge, *St. John 11124* (BISH); Paalaa Ridge, *Caum s.n.* (BISH); Paalaa, forested ridge s. of Opaepala Gulch, *Fosberg 10302* (BISH); South Opaepala Gulch, below crest of s. ridge, *St. John 12103* (BISH); South Opaepala Ridge, middle forest, *Suehiro s.n.* (BISH); Kaluanui, *St. John 10109* (BISH); between Punaluu and Kaipapau, *Forbes s.n.* (BISH); Punaluu, open hillside, *Hume 103* (BISH); Punaluu, *Degener 9785* (US); Punaluu-Wahiawa ridge, *Judd s.n.* (BISH); Poamoho Trail, *Oliveira 52* (US); Wahiawa gulches, *Forbes 1711 O* (BISH); Wahiawa, Kahana Trail, *Forbes 2205 O* (BISH); Kahana Valley Ditch Trail, *Fosberg 10402* (BISH); Waikane-Schofield Trail, near top of divide, *St. John 10177* (BISH); Waikane-Schofield Trail, *St. John 12123* (BISH); Waipio, Kipapa Gulch, *Fosberg 9548* (BISH); s. ridge of Kipapa Gulch, *Hosaka 1014* (BISH), *Yamaguchi 1237* (BISH); Halawa Valley Ridge Trail, *Cowan 556* (BISH), *N293*; Honolulu, *U.S. Expl. Exped.* (US 690602); Palolo Valley, *Skottsberg 910* (BISH); Palolo-Waialae ridge, *Fosberg 13133* (BISH). Koolau Mts. (without definite locality): *Forbes s.n.* (BISH). Oahu (without definite locality): *Remy 156* (P), *Macrae s.n.* (K). MOLOKAI: Waikolu Valley, *Krajina s.n.* (BISH, US 1991819); along trail to Pepeopae Bog, *N261*; Wailau pali, *Rock s.n.* (A, BISH); Wailau-Mapulehu divide, edge of cliff, *Fosberg 13509* (BISH); ridge e. of Mapulehu Valley, *St. John & Fosberg 12874* (BISH); Puniuohua, *Munro 697* (BISH), *531* (BISH); Halawa, *Hillebrand* (*Herb. Lugd. Bat. 903.248 54*) (L). Molokai (with-

out definite locality): *Forbes 285 Mo* (BISH). MAUI. West Maui: Kalaeokaea, *Forbes 2550 M* (BISH, US); Honokohau drainage basin, *Forbes 499 M* (BISH). East Maui: Kailua, *Lyon s.n.* (BISH), *Rock s.n.* (BISH); Waikamoi area, wet forest at rim of gulch, *N258*; Keanae Trail, *Rock s.n.* (A, BISH); ditch trail s. of Keanae, *Munro 487* (BISH), *664* (BISH); Nahiku, *Forbes 245 M* (BISH); ridge on left side of Kipahulu, *Forbes 1641 M* (BISH); w. part of Kipahulu Valley, *Lamoureux & DeWreede 3860* (BISH); near Hana, Puu Ki, *St. John & Catto 17879* (BISH). Maui (without definite locality): Upper ditch trail, *Lyon s.n.* (BISH); Mahikee, *Faurie 1161* (P). HAWAII: Honomu, canyon bottom in hills above Akaka Falls, *Fosberg 10475* (BISH); Hilo, *Hillebrand & Lydgate s.n.* (BISH); Kulani Road, ne. of Kulani Honor Camp, *N138, 139, 140*; Kulani Road, Upper Waiakea Forest Reserve, *Hatheway 440* (BISH); between Glenwood and Volcano House, *Degener 30213* (BISH). Hawaiian Islands (without definite locality): *U.S. Expl. Exped.* (US 809272), *Remy 156* (A).

1b. *Joinvillea ascendens* subsp. *samoensis* T. K. Newell, subsp. nov.  
FIG. 4C; FIG. 5C.

*Joinvillea gaudichaudiana* sensu Christophersen, Bishop Mus. Bull. 128: 46, p.p. 1935.

Herba erecta 2–4 m. alta, caule tereti, nodis distalibus 4–6 mm. diametro, internodiis distalibus 6–14 cm. longis; vagina tereti; auriculis ad 6 mm. longis oblongis apice rotundatis vel paulo acutis; foliorum laminis 6.5–13 cm. latis utroque costae 9–12-plicatis; supra trichomatibus raris uni- et multicellularibus etiam setis raris vel infrequentibus; subtus setis raris vel frequentibus. Inflorescentia villosa etiam trichomatibus erecto-patentibus brevibus rigidis aliquam ornata, ramulis primariis medium versus 0.9–1.3 mm. diametro, ramulis ultimis apicem versus 0.3–0.5 mm. diametro; tepalis exterioribus 2.1–3 mm. longis apice mucronulatis vel mucronatis et interdum reflexis, tepalis interioribus 1.9–3 mm. longis. Stylis persistentibus; fructibus 4.1–5.6 mm. diametro.

TYPE: North rim of Lake Lanutoo Crater, Upolu, Western Samoa, at 700 meters elevation, *Newell 239* (BISH holotype) 26 October, 1966.

DISTRIBUTION. Endemic and so far recorded only from Western Samoa, from elevations of 700 to 1,600 meters, in wet forests and often in shaded localities.

Western Samoa. SAVAII: Forest ne. of Samataitai, *N247, 248, 249*; ne. of Salailua, *Christophersen 2562* (BISH); crater rim above Matavanu Crater, *Christophersen & Hume 2206* (BISH, NY, US); forest above Matavanu Crater, *Christophersen & Hume 2030* (BISH, US); forest sw. of Matavanu Crater, *N245*. Savaii (without definite locality): *Whitmee 245* (K); *U.S. Expl. Exped.* (US 690600). UPOLU: Lake Lanutoo, *Christophersen 122* (BISH, NY), *372* (BISH), *Hochreutiner 3269* (L); n. rim of Lake Lanutoo Crater, *N235, 237, 238, 239* (BISH holotype), *240, 241, 242, 243, 244*. Upolu (without definite locality): *Reinecke 305* (BISH). SAMOA (without definite locality): *Whitmee 23* (K), *s.n.* (A, K).

- 1c. *Joinvillea ascendens* subsp. *borneensis* (Beccari) T. K. Newell, comb. nov. FIG. 4A; FIG. 5A.

*Joinvillea borneensis* Beccari, Nelle Foreste di Borneo, 198. 1902; Merrill, Enum. Philip. Fl. Pl. 1: 190. 1923; Backer, Fl. Males. I. 4: 245. 1951.

*Joinvillea malayana* Ridley, Jour. Straits Branch Roy. Asiatic Soc. 44: 199. 1905; Fl. Malay Pen. 4: 368. 1924.

Erect herb, 2–5.5 m. high; stem terete, 4–9 mm. in greatest diam. at distal nodes, the distal internodes 5–11.5 cm. long; sheath terete; auricles to 14 mm. long, oblong, rounded at apex; lamina with 9–13 plications on each side of midrib, 5–14 cm. broad; unicellular and multicellular trichomes on abaxial laminal surface rare to infrequent; bristles infrequent to frequent on both surfaces. Inflorescence with erecto-patent short stiff trichomes, primary branches 0.7–1.2 mm. in diam. at midpoint, ultimate branchlets 0.3–0.5 mm. in diam. 5 mm. from tips; outer tepals 1.7–2.8 mm. long, with a mucronulate, rarely reflexed, tip; inner tepals 1.8–2.6 mm. long. Styles persistent on fruit; fruit 3.4–4.8 mm. in diam.

TYPE: Since neither Beccari nor subsequent workers indicated a type I am choosing *Beccari 2816* (FI) as lectotype. This specimen is from Gunung Wa, Sarawak, East Malaysia, the type locality, and may have been part of Beccari's original collection. He reported finding the new species on 19 November, 1866 (Beccari, 1902); the label of *Beccari 2816* bears the date November, 1866. The specimen chosen is in mature fruit with the perianths in good condition.

LOCAL NAMES. In West Malaysia known as "rotan bini" (Backer, 1951), a name apparently shared with *Flagellaria indica* L. (Ridley, 1924). The name "si marboeloe-boeloe" on the label of *Rahmat si Boeea 5921* (L), a specimen collected on Sumatra. In the Philippines called "odyung" in Tagbanua (Backer, 1951).

DISTRIBUTION. Malay Peninsula (West Malaysia), Sumatra, Borneo (Sabah and Sarawak in East Malaysia and Kalimantan), the Philippine Islands (Jolo and Palawan), and the Caroline Islands (Ponape), from about 50 to 1,920 meters elevation. Growing along roadsides, forest edges, and other partially open, wet but well drained sites; common as a pioneer plant in open roadcuts near the Sabah National Park (SNP) Headquarters.

Malaysia. WEST MALAYSIA. Perak: Taiping Hills, *Ridley 11916* (K); Maxwell's Hill, mile 8, *N164*; G. Hijau, near summit, *N161, 162, 163*; G. Batu Puteh, *Wray 253* (K). PAHANG. Cameron Highlands: *Md. Nur SF 32579* (A); n. of Brinchang, along trail to G. Batu Brinchang, *N165*; along road to G. Batu Brinchang, *N166, 167, 168, 169*; along road ne. of Brinchang, *N170, 171*; along road between Brinchang and Tanah Rata, *N172*. SELANGOR (at border): Fraser's Hill, *Burkill & Holttum SF 8649* (K), *N173, 174, 175*; Fraser's Hill, gap road, *Purseglove 4124* (L); Semangkok Pass, *Ridley s.n.* (K). EAST MALAYSIA. Sabah: near Jesselton, Hulu Inanam, *Otik SAN 4165* (K); along Tamparuli-Ranau road, mile 14, *N157*; mile 18, *N156*; mile 19, *N155*; mile 20, *N153*,

154; mile 21, N152; vicinity of SNP Headquarters, N144, 149, 150, 151; along Tamparuli-Ranau road, mile 35.5, N145, 146, 147, 148; mile 37, N143; Mt. Kinabalu, Bungal Trail, J. & M. S. Clemens 26015 (A, K, L, NY); Mt. Kinabalu, Gurulau Spur, M. S. Clemens 10799 (A); Mt. Kinabalu, Pinosuk Plateau, Chew, Corner & Stainton 1809 (K). Sarawak: G. Wa, Beccari 2816 (FI, 2 specimens, including lectotype, in fruit; K). Sarawak (without definite locality): native collector SAR 1707 (A, K, US).

**Indonesia.** SUMATRA: Atjeh, Gajolanden, van Steenis 8784 (A, L); trail from Medan road to top of Sibajak Volcano, W.N. & C.M. Bangham 1025 (A, NY); Sibajak, Lörzing 13893 (K, L), Stomps (Herb. Lugd. Bat. 948.59 441) (L); Tapianoeli, Rahmat si Boeea 5921 (L); Air Putih, e. of Pajokumbuh, Alston 14375 (L). Sumatra (without definite locality): Alston 14787 (L), Bunnemeyer 8695 (L), collector unknown (Herb. Lugd. Bat. 925.206 829) (L). KALIMANTAN: Central East Borneo, West Koetai, Endert 4502 (A, K, L).

**Philippine Islands.** PALAWAN: Mt. Capoas, Merrill 9515 (BISH, K, L, NY, US); Brooke's Point, Mt. Mantaliñgahan, Edaño 119 (L), 1050 (A). Palawan (without definite locality): Foxworthy 42135 (US).

**Caroline Islands.** PONAPE: Kuporujō (Mt. Kuprish), Takamatsu 667 (BISH).

1d. *Joinvillea ascendens* subsp. *glabra* T. K. Newell, subsp. nov.

FIG. 4B; FIG. 5B.

Herba erecta 1.5–2.5 m. alta, caule lateraliter compresso raro tereti, nodis distalibus 5–11 mm. diametro, internodiis distalibus 3.6 cm. longis; vagina lateraliter compressa raro tereti; auriculis ad 40 mm. longis subulatis raro oblongis; foliorum laminis 4.5–7 cm. latis utroque costae 7–9-plicatis; supra trichomatibus raris plerumque multicellularibus et ramulosis; utrinque setis raris. Inflorescentia trichomatibus erecto-patentibus brevibus rigidis ornata etiam interdum parce villosa, ramulis primariis medium versus 0.9–1.3 mm. diametro, ramulis ultimis apicem versus 0.3–0.5 mm. diametro; tepalis exterioribus 1.9–3 mm. longis apice mucronulatis raro reflexis, tepalis interioribus 1.9–2.6 mm. longis. Stylis persistentibus; fructibus 3.3–4.6 mm. diametro.

**TYPE:** Plateau de Dogny, New Caledonia, edge of gallery forest at 950 meters elevation, Newell 196 (BISH holotype) 1 October, 1966.

**DISTRIBUTION.** Endemic to New Caledonia, and so far known only from the vicinity of the Plateau de Dogny, from elevations of 720 to 980 meters. Growing mainly at the forest edges in wet but generally well-drained areas.

**New Caledonia.** Plateau de Dogny, at edges of forested areas on the Plateau, N196 (BISH holotype), 198, 199, 200, 201, 202; somewhat open forest on slopes sw. of the Plateau, N192, 193, 194.

2. *Joinvillea plicata* (Hook. f.) T. K. Newell & B. C. Stone, *Taxon* 16: 193. 1967.

*Flagellaria plicata* Hook. f., Hook. Jour. Bot. Kew Gard. Misc. 7: 200. *pl.* VIII. 1855.

Erect herb, 1.5–5.5 m. high; auricles to ca. 90 mm. long; lamina with

variable trichomes on the abaxial surface, bristles on adaxial surface frequent to abundant, 8–15 plications on each side of midrib, 50–100 cm. long and 5–20 cm. broad when flattened. Tepal apex usually not splitting in age; outer tepals deltoid-lanceolate with an acute to acuminate tip, with 1 central vein and sometimes 1 or 2 lateral veins, 1.7–3.1 times longer than broad, 1.7–4.1 mm. long and 0.8–1.9 mm. broad; inner tepals deltoid-lanceolate to ovate with an acute to acuminate apex, 1–2 times longer than broad, 1.1–3.3 mm. long and 0.8–2.1 mm. broad. Styles usually persistent on fruit; fruit 4–6 mm. in diam.

2a. *Joinvillea plicata* subsp. *plicata*.

FIG. 4E–I; FIG. 5E–G.

*Flagellaria plicata* Hook. f., Hook. Jour. Bot. Kew Gard. Misc. 7: 200. *pl.* VIII. 1855.

*Joinvillea elegans* Gaud. Atlas, Voy. Bonite. *pl.* 39 & 40, fig. 7–26. 1841, *nomen nudum*; Brongn. & Gris, Bull. Soc. Bot. France 8: 268. 1861.

*Flagellaria elegans* Seem. Fl. Vit. 315. 1868.

Erect herb 1.5–5.5 m. high; stem terete to bilaterally compressed, 5–14 mm. in greatest diam. at distal nodes, distal internodes 2–11 cm. long. Leaf sheath terete to bilaterally compressed; auricles to ca. 90 mm. long (mostly 15 mm. or less), oblong, rounded at apex, sometimes subulate, mostly straight. Lamina 50–100 cm. long and 5–20 cm. broad, apex acute to attenuate; variable trichome types on abaxial surface infrequent to abundant; multicellular trichomes on abaxial veins rare to abundant (mostly infrequent to frequent). Inflorescence 3–5 times branched, 10–40 cm. long and 9–40 cm. broad; outer tepals 1.7–3.6 mm. long and 0.8–1.9 mm. broad, sometimes with 2 lateral veins; inner tepals 1–2 times longer than broad, 1.1–3.1 mm. long and 0.8–1.9 mm. broad; fruit globose to somewhat dorsiventrally flattened, 1.1–1.7 times broader than high, 4–6 mm. in diam.

TYPE: Île des Pins, New Caledonia, *Macgillivray* 770 (κ lectotype). Hooker (1855) cites two specimens, *M'Gillivray* (*Macgillivray*) and *Milne*, October 1853 (young fruit). I have examined them and found both in good condition with young fruit; *Macgillivray* 770 is here selected, because the herbarium sheet also bears drawings of fertile structures appearing in the plate accompanying Hooker's description.

LOCAL NAME. Called "wahedali" on the label of *Brass* 3254 (BISH) from Santa Ysabel. BSIP.

DISTRIBUTION. Solomon Islands (Santa Ysabel, Guadalcanal, and San Cristóbal), New Caledonia proper and Île des Pins, New Hebrides (Aneityum), and Fiji (Viti Levu, Vanua Levu, and Taveuni), from near sea level to 1,195 meters elevation. Frequently found in the Solomon Islands and Fiji, and forming a conspicuous part of the New Caledonian flora. *Joinvillea elegans* Gaud., as illustrated in Gaudichaud (1841), clearly belongs here, and most closely resembles New Caledonian specimens. Gaudichaud's specimen was lost and its collection locality is un-

known. Since the Bonite did not stop at any of the islands where this taxon is known to occur, a specimen was probably sent to Gaudichaud. However, he may have collected it on a previous visit to the New Caledonia area.

Subspecies *plicata* is quite variable, but the New Caledonian plants overlap so strongly with those of the Solomon Islands and Fiji, that I find no good basis for recognition of additional subspecies. Although several varieties of subspecies *plicata* might be distinguished in New Caledonia, it seems inadvisable to suggest these without additional material and more detailed field investigation.

**British Solomon Islands Protectorate.** SANTA YSABEL: Kakatio, *Brass* 3254 (A, BISH). GUADALCANAL: Nw. end of island on ridge above Hidden Valley, *N176, 177, 178, 179, 180, 181*; Gold Ridge, up from bungalow, *Whitmore BSIP 646* (L). SAN CRISTÓBAL: Hinuahaoro, *Brass* 2908 (A, BISH, L).

**New Caledonia.** Wagap, *Vieillard 1396* (A, FI, K, L, NY); at edge of forested area on Plateau de Dogny, *N197*; open forest just below sw. edge of Plateau de Dogny, *N195*; forested slopes sw. of Plateau de Dogny, *N190, 191, 203*; Pirogue, *MacDavids & Barrau 2449* (P); auf den bergen bei Païta, *Schlechter 14870* (L); La Dumbéa, *Franc 27* (US); Mt. Koghi, Route de l'Hermitage, *N184, 186, 187, 188, 189*; Kae (Caferie), *Chabert s.n.* (FI); ne. of Conception, *Balansa 944* (P); Nouméa, *Cribes 897* (A, NY); along road from mouth of Lembé R. to Mts. Kouanenoa, *N215, 216, 217, 218, 219, 221, 222, 223, 224, 225*; base of Mt. Dore, *Buchholz 1009* (US); Prony, *M. et Mme. Le Rat 1599* (P, US); Baie de Prony, *Godefroy* (Herb. Lugd. Bat. 951.74 740) (L); Isle of Pines, bank of stream, *Milne 172* (K), by stream in a wood, *Macgillivray 770* (K lectotype), on bank above small stream about 2 km. nw. of Pic Nga, *N205, 206, 207, 208, 209, 210, 211, 212, 213, 214*. New Caledonia (without definite locality): *Baumann-Bodenheim 5016* (A), *Deplanche 358* (P), *Franc 27* (NY), *Le Rat 2467* (A), *Germain* (US 1506846), *s.n.* (A, K), *Pancher s.n.* (K, NY).

**Fiji.** VITI LEVU. Mba: Mt. Evans Range, Mt. Koroyanitu, *Smith 4182* (BISH, L, US); w. of Nandarivatu, Mt. Ndelaiyoö, *Smith 5080* (A, BISH, L, US); along road in vicinity of Nandarivatu, *N234*; inland from Navai, *Reay 862* (A); Navai, Vuninatambua, *Degener 14876* (A, NY). Mba or Naitasiri: Between Nandarivatu and Nasonggo, *Reay 34* (A). Serua: Between Ngaloa and Korovou, *Smith 9247* (US); along road n. of Ngaloa, *N227, 228, 229, 230, 231, 232, 233*; vicinity of Ngaloa, *Degener 15139* (A, BISH, L, NY, US); e. of Navua R., *Smith 9121* (US). Namosi: Hills between Navua R. and Suva, *Greenwood 1008* (A, BISH). Naitasiri: Rairaimatuku Plateau, *Smith 6113* (A, US); along Sawani-Serea road, *N226*. Viti Levu (without definite locality): *Seemann 645* (A, K). VANUA LEVU. Mbua: Navotuvotu, Mt. Seatura summit, *Smith 1642* (BISH, NY, P, US). Mathuata: Ndreketi, *Parham et al.* (Fiji Dept. Agric. 13456) (K). Thakaundrove: Eastern drainage of Yanawai R., *Degener & Ordonez 14063* (A, BISH, NY, US); Mt. Mbatini, crest of range, *Smith 655* (BISH, NY, US). Taveuni: Trail from Somosomo, *Gillespie 4820* (BISH). Fiji (without definite locality): *Yeoward 27* (K).

2b. *Joinvillea plicata* subsp. *bryanii* (E. Christophersen) T. K.  
Newell, comb. nov. FIG. 4I; FIG. 5H.

*Joinvillea bryanii* Christophersen, Bishop Mus. Bull. 128: 44. 1935.



Erect herb, 3–5.5 m. high; stem terete, 4–8 mm. in greatest diam. at distal nodes, distal internodes 6–7 cm. long. Leaf sheath terete; auricles to 12 mm. long (mostly 6 mm. or less), somewhat oblong, rounded to acute at apex, apex mostly curving away from ligule. Lamina 52–74 cm. long and 6–15 cm. broad, apex attenuate; trichomes on abaxial surface unicellular and some multicellular, mostly abundant; multicellular trichomes on abaxial veins frequent to abundant. Inflorescence 3–4 times branched, 11–22 cm. long and 10–25 cm. broad; outer tepals 2.9–4.1 mm. long and 1.2–1.8 mm. broad, usually without lateral veins; inner tepals 1.3–2 times longer than broad, 2.5–3.3 mm. long and 1.5–2.1 mm. broad; fruit globose, 1.2–1.3 times broader than high, 4.3–5.4 mm. in diam.

TYPE: Forest above Aopo, Savaii, Western Samoa, at 900–1,000 meters elevation, *Christophersen 3457* (BISH holotype) 7 December, 1931.

LOCAL NAME. Called "ū vao" on the label of *Christophersen 2714*.

DISTRIBUTION. Endemic, and so far recorded only from Savaii, Western Samoa, from elevations of 800 to 1,500 meters, in wet forests and often in shaded localities.

Subspecies *bryanii* is a very homogeneous taxon but does not differ strongly from some Fijian and New Caledonian material. The extent of overlap, seems to justify the reduction of this taxon to the rank of subspecies. Its uniformity and the fact that it has been found only on Savaii indicate that it may be a relatively recent arrival in Western Samoa and might be considered a peripheral isolate. It probably arrived as a single introduction; lack of variation could be a result of a small gene pool.

Western Samoa. SAVAII: Forest ne. of Samataitai, *N250, 251, 252, 253, 254, 255*; forest above Aopo, *Christophersen 3457* (BISH holotype, P isotype); above Salailua, forest slopes above Papafu Crater, *Christophersen 2682* (BISH); forest just below rim of Papafu Crater, *Christophersen 2714* (BISH); forest above Salailua, *Christophersen 2747* (BISH), *3097* (BISH, US); rain-forest above Safune, *Bryan 125* (BISH, NY); forest above Matavanu Crater, *Christophersen & Hume 2040* (BISH, US), *2088* (BISH), *2283* (BISH).

TABLE 1. Chromosome numbers in *Joinvillea*

SPECIES	COLLECTION CHROMOSOME		LOCALITY
	NUMBER	NUMBER	
<i>J. ascendens</i>			
subsp. <i>borneensis</i>	N170	$n = 18$	G. Brinchang, West Malaysia
subsp. <i>borneensis</i>	N146	$n = 18$	SNP, East Malaysia
subsp. <i>glabra</i>	N201	$2n = 36$	Plateau de Dogny, New Caledonia
subsp. <i>ascendens</i>	N139	$n = 18$	Hawaii, Hawaii

THE ECOLOGY OF AN ELFIN FOREST IN PUERTO RICO, 9.  
CHEMICAL STUDIES OF COLORED LEAVES

RICHARD J. WAGNER, ANTISS B. WAGNER, AND RICHARD A. HOWARD

ONE OF THE SPECTACULAR FEATURES of tropical vegetation is the frequent occurrence of brightly colored leaves. The color may be found in young foliage, produced either regularly or seasonally, or in the mature foliage of certain taxa as common in cultivation as *Codiaeum variegatum* var. *pictum* or *Acalypha wilkesiana*. Color development in the fall or with the change from dry to rainy season is less frequent. The red colors are assumed to be due to the dominance of anthocyanin pigments and may appear in young leaves before the chlorophyll develops, in mature leaves in segments of the blade or partially masked by chlorophyll, and in senescent leaves after the chlorophyll has been destroyed. Red color may also be a pathological symptom frequently associated with phosphorous deficiency. Macmillan (1952) stated "anthocyanin may appear temporarily in the young leaves, and, if abundant before the chlorophyll is largely developed, a bright red immature foliage results. This is very evident in many tropical trees, e.g. *Mesua ferrea*, a species of *Calophyllum*, *Eugenia*, *Cinnamomum* etc. The coloration is at times so vivid that from a distance such trees appear to be in flower." Anthocyanins are usually red in acid solution and may become purplish to blue as the pH is increased. A previous paper (Howard, 1969) has shown that the pH of the plant sap of the component species of the elfin forest on Pico del Oeste ranges from 2.5 to 6.5. Anthocyanins are often associated as well with the occurrence of sugars in the plant cells and, in temperate areas, with the occurrence of frost or low temperatures. Crocker (1938) stated "anthocyanins appear in many plant cells mainly in the early spring and in autumn at times of low temperatures; under these conditions soluble sugars are also abundant in plant organs. Arthur finds that low temperature favors the development of anthocyanin in the apple without a change in sugar content. He also points out that the small amount of pigment found in cells calls for relatively little sugar as a building material and concludes that temperature probably acts directly rather than through sugar accumulation." More recent work has shown an association of color due to anthocyanin with a shortened photoperiod and suggests that it may be regulated by a phytochrome system. Finally it is evident to anyone familiar with a fall season in New England that potential for the development of color is also inherent in certain plants.

The elfin forest on Pico del Oeste displays a localized brilliance in the vivid colors of young leaves and in the flush growth of many of the woody components. The development of color with age was noted only

in *Miconia pachyphylla*, *Mecranium amygdalinum*, and *Calycogonium squamulosum*. Perhaps the greatest year-round color, however, is found in many plants of the bromeliad genus *Vriesea*.

We were not able to attempt tests of the ratio of red to far-red light as a factor in the leaf color we observed in the various plants of the cloud-dominated environment. We were able, however, to establish a small laboratory through the courtesy of Mr. Joseph Martinson, in which we attempted simple tests to examine the chemical bases previously proposed for the color we observed. Tests were run to determine the sugar content of young and old leaves, and of the red- and green-leaved forms of *Vrieseas*, and that of the water soluble phosphorus.

The epiphyte *Vriesea sintenisii* occurs throughout the forest: on the branches of isolated trees, on upper branches of trees forming the canopy, with many young plants on the horizontal branches or, occasionally, on the ground in cut-over areas. The plants that are exposed to the sky exhibit a brilliant red color. Within the forest, on shaded branches, and frequently on the ground other plants of the same species lack the red color and are pale green in appearance. Although the color difference is intense, the red plants may have the leaf bases green within the rosette but very few plants could be truly called intermediate, that is, partly green and partly red. The principal variation is in the intensity of red. The color difference is also apparent at a very young age. Seedling plants in exposed areas, with developing leaves, have red color at the tips while the protected or shaded seedlings are all green. The intensity of color does not appear to vary throughout the year or to suggest a photoperiod variation. However, the maximum variation in daylength during the year in Puerto Rico is only 2 hours and 18 minutes.

Gleason and Cook (1927) do not mention *Vriesea sintenisii* in their description of elfin forest types, and previous workers on the family or on the flora of Puerto Rico have not described the color variations or suggested any taxonomic value for them. Our initial encounter with these two color forms of *Vriesea sintenisii* suggested that two ecotypes were present.

The brilliance of the red form of *Vriesea sintenisii* suggested that the plants might make attractive ornamentals. However, when bright red plants were taken to a lower elevation within the Luquillo Mountains and placed in an area with less cloud cover, the plants died even when supplied with water daily. Red color forms which were returned to Boston and kept in the greenhouse under high humidity, without any adjustment of the natural photoperiod of the Boston area, retained their red color but failed to flourish, remaining in a vegetative state long after plants of comparable size on Pico del Oeste had flowered, shed seeds, and reproduced vegetatively. Red-colored plants taken from the exposed tree tops and placed on the forest floor in the shade gradually lost their red color and by the time of flowering were almost completely green.

The green-colored plants were also subjected to transplant experiments. These, too, failed to survive when transferred to a lower location, while

those transported to the greenhouse in Boston grew well in the new location and flowered on schedule when compared with plants on Pico del Oeste. Green-colored plants within the elfin forest were also transferred from their protected positions to exposed positions by strapping branches holding these plants to upper branches of the forest canopy. These green plants died in the exposed positions. Unfortunately we were unable to attempt a gradual transfer of these plants from one position to another. Clearly the green plants were physiologically adapted to shaded location and could not survive an abrupt although seemingly slight change in exposure to greater light. The red plants became adapted to the shaded location with the apparent loss or masking of the red pigment.

A second bromeliad found in the elfin forest was *Guzmania berteroniana*. Plants of *Guzmania* occurred primarily on the trunks of *Prestoea montana* or on the ground in protected areas on the lee slopes of the trail. All plants of *Guzmania* were green and no red forms were seen. Transplant experiments produced results nearly comparable to those for green forms of *Vriesea*. Plants taken to lower elevations died; those taken to Boston have persisted, but the rate of maturation was slower; plants which were transferred to exposed locations in the canopy died even more quickly than did the green forms of *Vriesea*.

When initial sugar tests suggested a higher sugar level in red-leaved plants of *Vriesea*, we continued a comparative study through two years, making analyses of plants in various stages of development.

In each test an average of eight plants was collected in the Pico del Oeste forest and taken to the laboratory. The leaves were all separated and washed thoroughly in running water and hand dried with towels. Roots and rhizomes were discarded. After the fresh weight of the leaves was obtained for each plant they were oven dried at 70°–75° for two days. When the dry weight was obtained the leaves were finely cut, and after a thorough mixing of the fragments of the individual plants, 1 gm. of dry leaves was placed in an Erlenmeyer flask; 100 cc. of distilled water was added; and the mixture was simmered for 30 minutes. When cooled to air temperature, distilled water was added to regain the original volume of 100 cc. The solution was allowed to mix for about two hours, then the sugar content was estimated quantitatively, following the colorimetric method of Folin and Wu (1920). In a second Folin-Wu tube 0.1 cc. of 1:10 diluted HCl was added and the tube submerged for 5 minutes in a boiling water bath to hydrolyze the higher sugars to a hexose before a second colorimetric sugar determination was made. The results are expressed in the following tables as percentages of sugar per gram of dry weight of the plant, and are the average of the eight plants of each sample category. There was no significant variation between the eight samples.

Soluble phosphorus determinations were made from 2 grams of the dried material which was diluted with 100 cc. of distilled water and simmered at 90°C. for 30 minutes; this was cooled to air temperature and distilled water was added to regain the original weight. The soluble

phosphorus was determined according to the procedure of Benedict and Theis (1924): 10 cc. of the extract and 10 cc. of a standard were mixed with 1 cc. of a 5% hypochlorate solution to decolorize the brownish mixture; after 24 hours the solution was filtered and 5 cc. of the standard and the unknown were measured in test tubes; the results are expressed as mg.% of dried plant material.

## 1966 RED-COLORED VRIESEA

COLUMN NO.	1	2	3	4	5	MEAN
WATER	83%	83%	83%	81%	80%	82%
HEXOSE	1.92%	1.88%	1.88%	1.44%	1.51%	1.73%
TOTAL SUGAR	2.27%	1.96%	2.05%	1.72%	1.96%	1.99%

## 1966 GREEN-COLORED VRIESEA

	1	2	3	4	5	MEAN
WATER	86%	85%	86%	85%	82%	84.8%
HEXOSE	1.27%	1.32%	1.29%	1.09%	1.36%	1.26%
TOTAL SUGAR	1.56%	1.82%	2.36%	1.15%	2.06%	1.79%

COLUMNS: 1. Young plants in vegetative rosettes. 2. Inflorescence present, basal flowers open. 3. Inflorescence mature, basal flower in young fruit stage. 4. Fruit forming, seeds turning black. 5. Fruiting stage, seeds mature.

## 1967 RED-COLORED VRIESEA

COLUMN NO.	1	2	3	MEAN
WATER	80%	85%	80%	82%
HEXOSE	1.5%	1.9%	1.8%	1.7%
TOTAL SUGAR	1.8%	2.1%	2.0%	2.0%
SOLUBLE PHOSPHORUS	23mg%	30mg%	21mg%	24mg%

## 1967 GREEN-COLORED VRIESEA

	1	2	3	MEAN
WATER	83%	86%	83%	84%
HEXOSE	1.2%	1.5%	1.4%	1.4%
TOTAL SUGAR	1.4%	1.7%	1.6%	1.6%
SOLUBLE PHOSPHORUS	26mg%	24mg%	25mg%	25mg%

COLUMNS: 1. Young plants. 2. Inflorescence mature. 3. Fruit mature.

## GUZMANIA BERTERONIANA

COLUMN NO.	1	2	3	4	MEAN
WATER	86%	85%	87%	88%	86%
HEXOSE	1.0%	1.1%	2.0%	1.2%	1.3%
TOTAL SUGAR	1.3%	1.3%	2.2%	1.2%	1.5%
SOLUBLE PHOSPHORUS	24mg%	25mg%	25mg%	n.e.	25mg%

COLUMNS: 1. Young vegetative rosettes. 2. Mature vegetative plants. 3. Inflorescence mature. 4. Fruits mature.

The water content of the leaf tissue of the components of the elfin forest has been given in a previous paper (Howard, 1969). Tissues tested contained from 93 percent water to 44 percent water. *Vriesea* ranked in